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Libyostrongylus dentatus n. sp. (Nematoda: Trichostrongylidae) from Ostriches in North America, with Comments on the Genera *Libyostrongylus* and *Paralibyostrongylus*

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LIBYOSTRONGYLUS DENTATUS N. SP. (NEMATODA: TRICHOSTRONGYLIDAE) FROM OSTRICHES IN NORTH AMERICA, WITH COMMENTS ON THE GENERA *LIBYOSTRONGYLUS* AND *PARALIBYOSTRONGYLUS*

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ABSTRACT: *Libyostrongylus dentatus* sp. n. is described from ostriches on farms from North Carolina and Texas. Nematodes were recovered from the posterior proventriculus and under the koilon lining of the gizzard; the parasites occurred in mixed infections with *Libyostrongylus douglassii*. The species is distinguished from congeners by the presence of a prominent, dorsal, esophageal tooth; in males by the structure of the dorsal ray and spicules; and in females by small eggs (52–62 μm in length), a sublateral vulva situated at 93% of the body length from the anterior, and a strongly curled, digitate, tail with cuticular inflations at the anus. Conflicts in the generic diagnoses of *Libyostrongylus* and *Paralibyostrongylus* were apparent, based on the structure of the dorsal ray or position of rays 3–5 of the copulatory bursa. These can only be resolved based on phylogenetic analyses of the 11 nominal species referred to these genera.

Although historically represented only in North American zoos, various species of ratites (emus *Dromaius novaehollandiae* [Latham], rheas *Rhea americana* Linnaeus, and ostriches *Struthio camelus* Linnaeus) have been gaining economic importance in the United States and southern Canada. Semiconfined to near free-ranging flocks are now widely distributed on ranches across temperate North America. Concurrent with more intensive husbandry of these avian species has been the renewed recognition of parasitism by helminths as an influence on production, morbidity, and mortality, e.g., Thieler and Robertson (1915), Barton and Seward (1993), and Button et al. (1993). Also it has become apparent that a substantial component of the typical parasite faunas (principally strongylate nematodes) associated with these hosts has been introduced from sub-Saharan Africa and South America and some pathogenic species now may be widely established in North America (Table I). Although the parasite faunas of ratites appear to be host specific and historically defined by biogeographic and host associations (Clay, 1957), the potential for cross-transmission to domesticated birds or avian taxa endemic to North America has yet to be established (nor has the reciprocal been considered in detail). The greatest potential for transmission resides with strongylate nematodes with direct life cycles.

This burgeoning interest in ratites and their parasites has resulted in numerous submissions to the U.S. National Parasite Collection for confirmation or identification. Recently, material was submitted from isolated flocks of ostriches in North Carolina and Texas, with a provisional identification of *Amidostomum* sp. based on the presence of a prominent esophageal tooth extending into the buccal cavity. It was later determined that these specimens represented a previously unrecognized species of *Libyostrongylus* Lane, 1923 (Trichostrongylidae: Libyostrongylinae), which is described herein. Additionally, we provide the basis for readily distinguishing all species of *Libyostrongylus* from ostriches, enabling rapid diagnosis, and comment on diagnostic characters for the genera *Libyostrongylus* and *Paralibyostrongylus* Ortlepp, 1939.

MATERIALS AND METHODS

Specimens of *Libyostrongylus* were collected at the time of necropsy from 2 adult ostriches on farms in North Carolina and Texas. Nematodes were fixed in buffered 10% formalin and later transferred to 70% ethanol and 5% glycerine. Entire specimens were studied using interference contrast microscopy after clearing in phenol–alcohol or in glycerine. Following clearing, transverse sections cut by hand with a cataract knife were prepared from a female specimen to allow determination of the presence or absence of a synlophe. The cephalic, vulval, and caudal extremity of 2 female specimens, prepared for scanning electron microscopy (SEM) via critical point drying, were mounted on stubs and sputter-coated with gold–palladium. These specimens were examined with an Hitachi S-5700 electron microscope at 10 kV at magnifications of 300–6,000×. In the description, measurements in μm were based on 10 males and 10 females, including the holotype and allotype. These data are presented as a range for all specimens, with the mean ± 1 SD in parentheses. Sample sizes for measurements of spicules and eggs are 20 and 50, respectively. Description of the copulatory bursa and numbering of the bursal rays follows Chabaud et al. (1970) and Durette-Desset (1983). The type series and representative specimens were deposited in the U.S. National Parasite Collection, USDA, ARS, Beltsville, Maryland.

Specimens of other species were examined for comparative purposes as follows: (1) *Libyostrongylus douglassii* (Cobbold, 1882), USNM 40741, specimens designated as *Ornithostrongylus douglassii* collected by H. O. Monnig, from the proventriculus (reported as stomach) of *Struthio australis* Gurney (now *S. camelus australis*) in Onderstepoort, South Africa; (2) *L. douglassii*, USNM 83439, 83827 from the proventriculus of *S. camelus* in Texas, collected by T. Craig; (3) *L. douglassii*, USNM 83828, from the proventriculus of *S. camelus* in North Carolina, collected by S. Lloyd; (4) *Libyostrongylus magnus* Gilbert, 1937, International Institute of Parasitology, LSHTM no. 1317 from *S. camelus* in Ethiopia, collected by S. G. Solomon, February 1933 (these specimens were labeled as *L. douglassii*, identity redetermined in the current study); and (5) *Paralibyostrongylus alberti* (Berghe, 1943), USNM 61421, specimens designated as *Libyostrongylus* from the stomach of *Dendrohyrax arbozéus adolphi* in Africa, collected by L. van den Berghe. Additionally, the correct spelling for the species originally described by Cobbold (1882) is *L. douglassii*, in accordance with Article 33, Part d, of the International Code of Zoological Nomenclature, 3rd ed. Subsequent spellings by various authors, including *L. douglasi* and *L. douglassi* are incorrect.

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TABLE I. Strongylate nematodes of rheas and ostriches introduced to North America based on the holdings of the U.S. National Parasite Collection.

	Rhea	Ostrich
*Deletrocephalus** *dimidiatus* Diesing 1851	Alabama 66136‡ Florida 56054‡ Missouri 82709 Maryland 82792	–
Paradeletrocephalus minor (Molin 1861)*	Washington, DC 27266‡	
Libyostrongylus† douglassii (Cobbold, 1882)	–	California 3204 Texas 83439, 83827 North Carolina 83828 New York 35417, 34654‡
Codiostomum† *struthionis* (Horst, 1885)	–	Texas 83751

* Host-specific parasite of rheas.
† Host-specific parasites of ostriches.
‡ Reported from animal park or zoo or captive situations.

RESULTS

Single ostriches from captive flocks in North Carolina and Texas were found to be infected with libyostrongyline nematodes in the proventriculus and gizzard. Two species of *Libyostrongylus* were found at necropsy and included gravid female specimens of *L. douglassii* and mature males and gravid females of a previously unrecognized species described herein.

Libyostrongylus dentatus n. sp.
(Figs. 1–14)

General description: Trichostrongylidae, uncoiled, red in life. Cuticle with strong transverse striations; synlophe absent. Cervical papillae minuscule, situated near level of excretory pore. Esophagus attains maximum diameter in posterior. Cephalic vesicle absent. Mouth oval, with dorsal and ventral notches; cuticularized buccal ring well developed. Prominent dorsal esophageal tooth present. In apical view, 6 cephalic papillae with 2 pairs near the lateral amphids, and 4 externo-labial papillae are apparent.

Male: Small nematodes with a prominent copulatory bursa. Total length 6,448–8,550 (7,522 ± 646.59), maximum width anterior to prebursal papillae, 105–140 (117 ± 10.03). Esophagus 483–569 (519 ± 31.57) long; maximum width attained at base, 36–55 (43 ± 31.57); ratio of total body length : esophageal length, 1:0.07. Nerve ring 192–304 (239 ± 33.48), excretory pore 265–369 (333 ± 33.12), and cervical papillae 265–387 (339 ± 37.95) from anterior.

Copulatory bursa symmetrical, of type 1-3-1. Bilateral cuticular inflations at level of prebursal papillae. Rays 2 shorter than rays 3–6. Distally, tips of rays 3 curved anteriad toward rays 2; tips of rays 3 and 4 in proximity; distally tips of rays 5 and 6 parallel and separate. Rays 8 arise at base of dorsal ray. Origin of rays 9 symmetrical or asymmetrical, arising as lateral processes in posterior half of dorsal ray; tips extending to posterior margin of bursal membrane. Distal to origins of rays 9, dorsal ray branches ending in terminal bifurcations of rays 10 and 11, often extending into rounded lobe of bursal membrane.

Spicules subequal, alate, 140–159 (147 ± 5.91) long; with main shaft ending in rounded point capped by hyaline sheath; narrow ventral and dorsal processes arising at 64–70% (68 ± 0.02%) of spicule length from anterior; spicule tips enveloped in membrane. Gubernaculum curved in lateral view, 49–59 (54 ± 3.40) in length. Genital cone complex, with single elongate "0" papilla ventral to cloaca, and paired "7" papillae contained in rounded plate, dorsal to cloacal aperture.

Female: Small nematodes with tail strongly curved ventrally. Total length 10,205–12,730 (11,488 ± 756.32); maximum width, 120–150 (137 ± 9.23), attained near level of vulva. Esophagus 447–610 (545 ± 46.75) long, maximum width attained at base, 36–55 (45 ± 5.44); ratio of total body length : esophageal length, 1:0.04–0.05 (0.05 ± 0.01). Nerve ring 200–285 (254 ± 28.41), cervical papillae 230–387 (323 ± 55.05), excretory pore 208–380 (326 ± 62.80) from anterior.

Ovaries didelphic. Vulva opens as transverse slit located sublaterally on the left or right side, slightly off ventral, at 9,525–11,835 from anterior extremity; at 92–93% of body length from anterior. Irregular, broad, cuticular inflations evident at level of vulva, disposed in ventral to sublateral fields adjacent to vulva, not extending anterior or posterior beyond vestibule; cuticular struts or other support not observed. Vagina vera short, dividing vestibule into long anterior and short posterior segments. Combined length of vestibule + sphincter 224–369 (290 ± 40.21) in anterior; 117–255 (210 ± 38.66) in posterior. Infundibula near equal in length, 91–213 (141 ± 32.64) in anterior; 78–200 (131 ± 33.57) in posterior. Total length of ovejector 702–933 (772 ± 70.60). Anterior uterine branch containing 29–71 (55 ± 14.36) eggs; posterior with 9–20 (14 ± 3.33). Eggs in early morula stage, 52–62 (57 ± 2.76) by 31–39 (34 ± 34). Tail 80–105 (92 ± 10.70) in length, strongly curled ventrally, with rounded, digitate tip; ventral cuticular inflation at level of anus.

Host: Type and only known host, *S. camelus* Linnaeus.

Habitat: Posterior proventriculus and under koilon lining of ventriculus; extending to caudal fourth of the ventriculus.

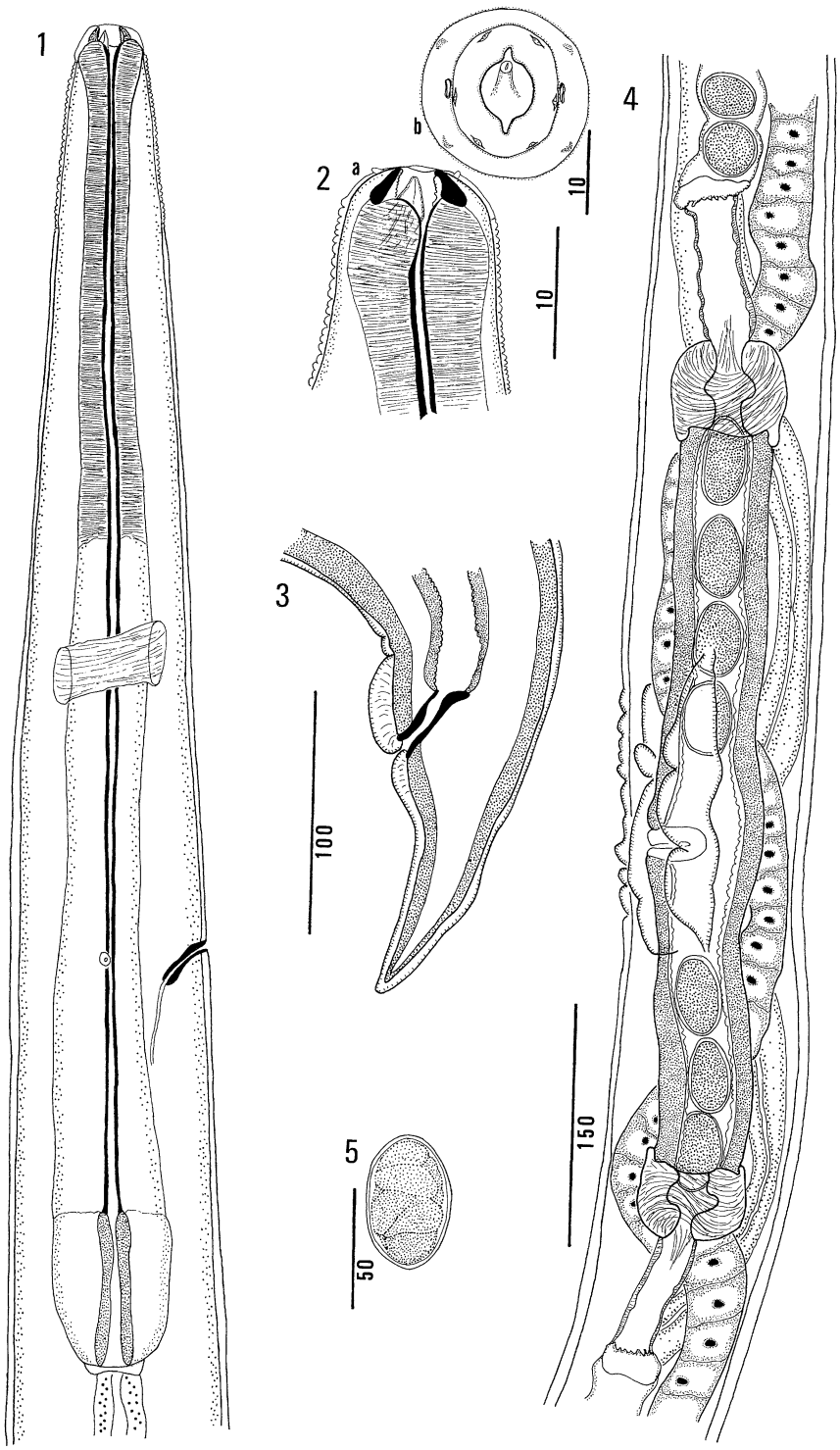
Specimens: Holotype male, USNM no. 83823, and allotype female, USNM no. 83824, from type host collected in North Carolina. Paratype specimens include 10 males and 9 females from North Carolina, USNM no. 83825; and 2 males from Texas, USNM no. 83752. Vouchers include 15 females from South Carolina, USNM no. 83826.

Locality: Reported from Lexington, North Carolina (type), and College Station, Texas; considered to represent a parasite introduced with the type host from sub-Saharan Africa.

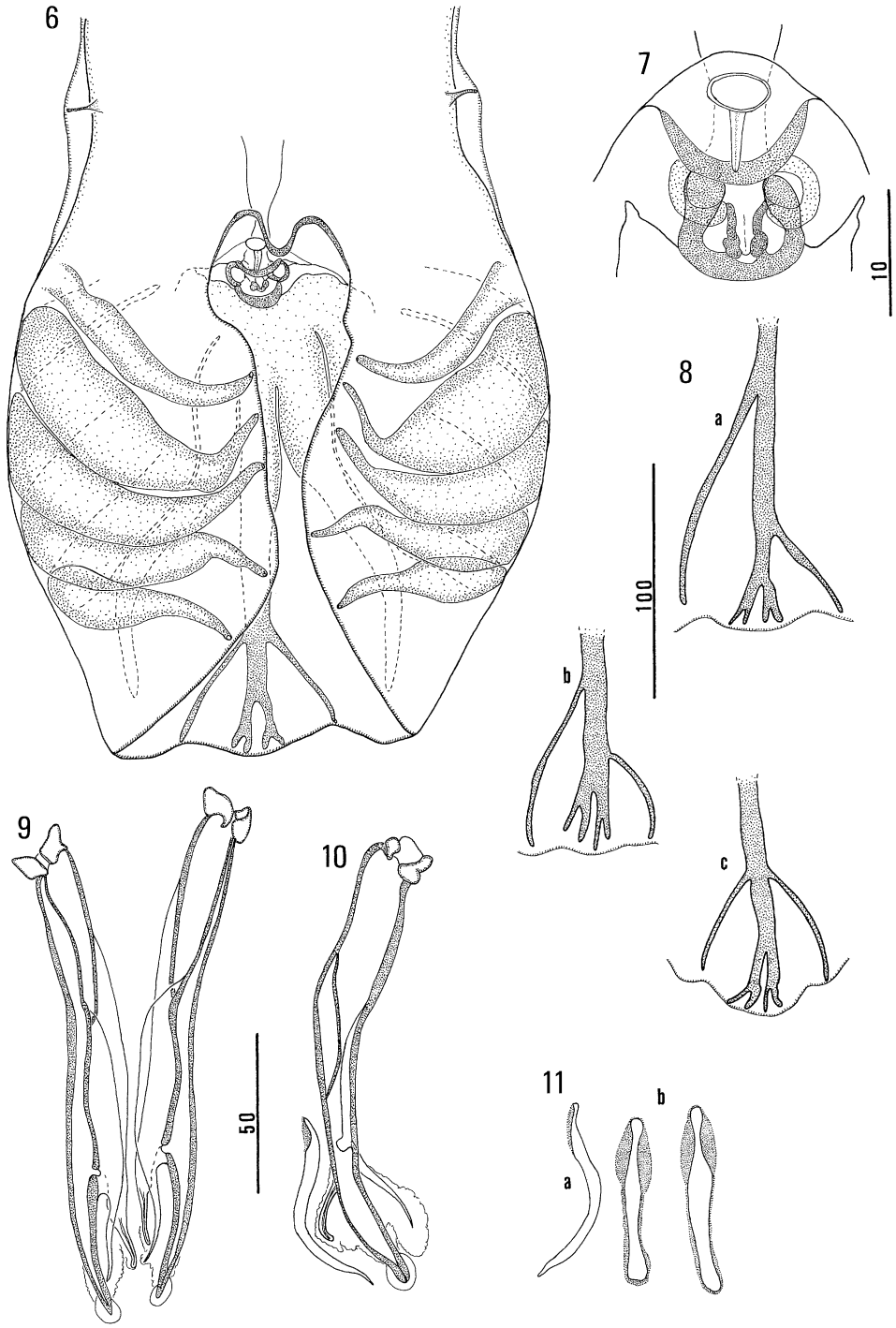
Etymology: The specific name "dentatus" refers to the prominent esophageal tooth.

Remarks: Currently there is disagreement over primary diagnostic criteria for *Libyostrongylus* and *Paralibyostrongylus* (see Puylaert, 1967; Gibbons and Khalil, 1982; Durette-Desset, 1983). Specimens of nematodes described herein are provisionally referred to the former genus based on the relative positions of the tips of rays 3, 4, and 5, where rays 3 and 4 are in proximity and distinctly separated from rays 5 (Durette-Desset, 1983). However, confusion over the adequacy of recognized criteria for these genera makes it necessary to provide comparisons among the 10 nominal species of *Libyostrongylus* (2) and *Paralibyostrongylus* (8).

Libyostrongylus dentatus n. sp. is distinguished from congeners, *L. douglassii* and *L. magnus* by the presence of a prominent, dorsal esophageal tooth, structure of the dorsal ray and female tail, a sublateral vulva positioned in the far posterior near the tail, small dimensions of eggs in utero, and other meristic characters (Tables II, III; Figs. 15–22). In *L. dentatus,* the dorsal ray resembles that of *Paralibyostrongylus* as presented by Ortlepp (1939) with rays 9 branching anterior to the bifurcation terminating in rays 10 and 11. Specimens of *L. douglassii*



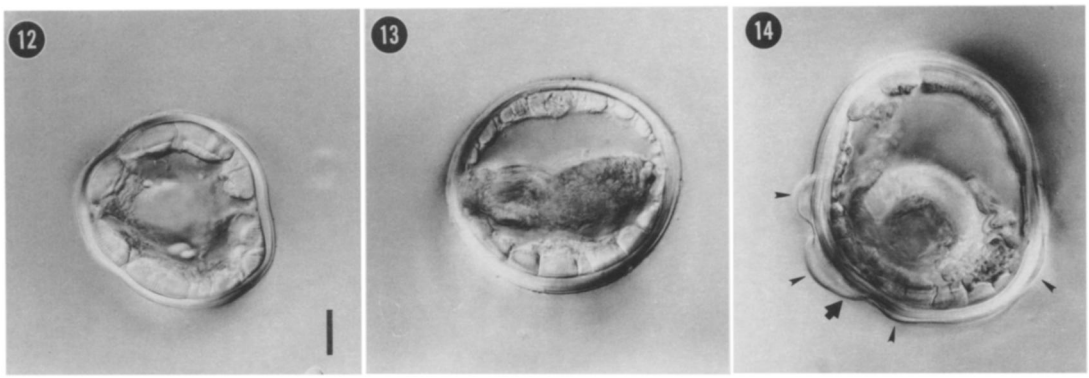
FIGURES 1–5. *Libyostrongylus dentatus* n. sp. from ostriches, *Struthio camelus*. Scale bars in μm; same scale for Figs. 1 and 3. **1.** Cephalic extremity and cervical zone in a female paratype. Right lateral view showing the structure of the esophagus, position of the nerve ring, excretory pore, and cervical papillae. **2a, b.** Cephalic extremity of allotype female. (a) Right lateral view showing structure of buccal cavity with well defined buccal ring and prominent dorsal esophageal tooth; (b) apical view, drawn from SEM of paratype, with dorsal oriented toward top of plate showing tooth, structure of oral aperture, and distribution of cephalic and externolabial papillae. **3.** Tail in a female paratype showing rounded tip and ventral cuticular inflations at anus. **4.** Ovejector and vulva in allotype female in left lateral view. Note structure of infundibula, sphincters, and vestibule; sublateral position of the transverse vulva; and broad cuticular inflations bordering the vulva. **5.** Egg in utero.



FIGURES 6–11. *Libyostrongylus dentatus* n. sp. from ostriches, *Struthio camelus*. Scale bars in μm; same scale for Figs. 6 and 8; and Figs. 9–11. **6.** Bursa, ventral view in paratype showing prominent inflations at level of prebursal papillae (rays 1), position of lateral rays 3 and 4 with distal ends in proximity, rays 8 arising at base of dorsal ray, and rays 9 branching anterior to distal bifurcation of rays 10 and 11 at extremity of dorsal lobe. **7.** Genital cone of holotype in ventral view showing single "0" papilla and complex "7" papillae and plate dorsal to cloacal aperture. **8a–c.** Dorsal rays, ventral view, showing variation in symmetry and position of branches of rays 9, 10, and 11. **9.** Spicules in a paratype ventral view, showing hyaline cap at apex of primary shaft, and ventral and dorsal processes extending from ala. **10.** Right spicule in lateral (external) view, showing structure of tips and relative position of gubernaculum. **11a, b.** Gubernaculum in lateral (a) and ventral (b) views.

examined in the current study were found to have a dorsal esophageal tooth; however, this attribute was poorly developed.

Compared to *L. douglassii,* male and female specimens of *L. dentatus* are larger. Among females, *L. dentatus* has a substantially longer ovejector, a greater number of eggs in the anterior uterus, a more posterior position of the vulva, markedly smaller eggs, a prominent cuticular inflation at the level of the anus, and a digitate tail (Tables II, III). Among males, spicule length is similar, but *L. dentatus* is readily iden-



FIGURES 12–14. *Libyostrongylus dentatus* n. sp. Structure of cuticle in female specimen as seen in transverse section; same scale for all figures, bar = 20 μm. **12.** Section at level of esophageal–intestinal junction. **13.** Section at level of midbody. **14.** Section at level of vulva (indicated by arrow) showing prominent cuticular inflations (pointers), not supported by cuticular struts, and without evidence of synlophe.

tified by the structure of the bursa and dorsal ray. Additionally, the presence of hyaline caps on the tips of the main shafts of the spicules in *L. dentatus* differs from the acutely pointed spicule tips of *L. douglassii.* Absence of marked sexual dimorphism, i.e., females smaller than males in *L. magnus,* smaller eggs, a more posterior vulva, a tail with cuticular inflation and smaller spicules distinguish *L. dentatus* from *L. magnus* (Tables II, III).

Published records of meristic data for *L. douglassii* require some comment (Tables II, III). Some measurements for *L. douglassii* in the literature are apparently incorrect. Thieler and Robertson (1915) indicated that the 50-μm length of egg reported by Cobbold (1882) was an artifact of fixation; thus, the range of measurements for this character would not overlap substantially with *L. dentatus.* Additionally, 800 μm for length of the ovejector reported by Skrjabin et al. (1954) represents an error in transcription from the work by Thieler and Robertson (1915). Consequently, the measurements presented for *L. douglassii* in the present study (Tables II, III) are compatible with those from the most detailed redescription by the latter authors.

Specimens of *L. douglassii* are recognized as particularly minuscule among the Libyostrongylinae. Thus, specimens of *Libyostrongylus* examined and redescribed by Durette-Desset and Denke (1978) are not compatible with all previous concepts for this species (Cobbold, 1882; Thieler and Robertson, 1915). These specimens differed substantially in the length of the body in males and females, dimensions of the esophagus (and relative length with respect to total body length), ovejector, spicules, and position of vulva (Tables II, III). Additionally, the females were reported as smaller than the males, a character only described for *L. magnus.* Thus, the material from ostriches in Somalia may be referable to *L. magnus* or a currently unrecognized taxon. Specimens of *L. magnus* examined in the current study were in agreement with the original description; sexual dimorphism was marked, eggs relatively large (near 85 μm in length), with a long ovejector, and spicule length ranging from 230 to 240 μm.

Specimens of *L. dentatus* resemble species of *Paralibyostrongylus* in the structure of the dorsal ray based on criteria by Ortlepp (1939) and Gibbons and Khalil (1982). Specimens of *L. dentatus* are distinguished from all nominal taxa of *Paralibyostrongylus* with respect to the arrangement of bursal rays 3–5, where the tips of rays 4 and 5 are in proximity in species of the latter genus (Table IV). Among species of *Paralibyostrongylus,* only *P. kalinae* Durette-Desset et al., 1992, has a prominent esophageal tooth, but spicules and eggs are considerably larger than in *L. dentatus.* Only in *P. cassonei* Durette-Desset and Denke, 1978 are eggs similar in dimensions to those of *L. dentatus,* but spicules differ markedly in males of these species (Durette-Desset and Denke, 1978) (Table IV).

DISCUSSION

Libyostrongylinae were not historically represented in avian hosts endemic to North America (Durette-Desset, 1985). It is clear, however, that at least 2 species of *Libyostrongylus* are now likely to be widely distributed in the United States (Table I), having resulted from transport and introduction of infected hosts.

Libyostrongylus dentatus n. sp. is considered to be a typical parasite of ostriches that should eventually be found in the historical range of the type host in sub-Saharan Africa. Due to the overall similarity and small size of *L. dentatus* and *L. douglassii,* it is suggested that the former species may have been overlooked previously. Difficulties in recovery of these nematodes would be compounded by their very small size and by localization in the proventriculus and under the koilon of the gizzard. Indeed, mixed infections of these species may not be uncommon and appear to be indicated by the observation of 2 distinct sizes of strongyle eggs, corresponding with these species (Table III), in ostriches from North Carolina, Mississippi, and Texas (pers. comm., L. G. Rickard and T. Craig). Although *L. douglassii* is known to be exceptionally pathogenic in ostriches (Thieler and Robertson, 1915; Button et al., 1993; Barton and Seward, 1993), the role of *L. dentatus* in morbidity and mortality remains to be determined. In the present paper, we provide the basis for clear differentiation of males and females of these species enabling accurate and rapid diagnosis (Tables II, III; Figs. 15–22). A third species, *L. magnus,* has not yet been reported in North America.

Specimens of *L. dentatus* can be unequivocally distinguished from species of *Libyostrongylus* and *Paralibyostrongylus* (Tables II–IV), but current morphological criteria at the generic level could allow placement in either genus (Gibbons and Khalil, 1982; Durette-Desset, 1983). Such could be construed as justification to reduce *Paralibyostrongylus* as a synonym of *Libyostrongylus* (see Chabaud, 1959; Le Van Hoa, 1959). However, the history of these genera and the distinct morphological characters on which they are based suggest that they are independent and that such a synonymy would be premature without detailed analysis.

The genus *Libyostrongylus* was established by Lane (1923) for some African trichostrongylids, with *L. douglassii* as type species from ostriches, and *L. hebrenicutus* Lane, 1923 from gorillas. Although superficially similar, these nematodes differed in the structure of the terminal bifurcations of the dorsal ray and in the pattern of the lateral rays (rays 3–5) of the copulatory bursa. This discrepancy led Ortlepp (1939) to establish the genus *Paralibyostrongylus,* naming *P. vondwei* Ortlepp, 1939 as the

TABLE II. Comparison of male Libyostrongylinae from ostriches, including *Libyostrongylus douglassii* (Cobbold, 1882) (1–4), *L. magnus* Gilbert, 1937 (5), and *L. dentatus* n. sp.; ranges with mean values in parentheses.*

Character	1	2	3	4	5	*Libyostrongylus dentatus* n. sp.
Total length	4,200–4,500	4,650	8,800	4,315–5,100 (4,679)	13,860–14,580	6,448–8,550 (7,522)
Esophagus length	480–500	480–500	680	426–465 (447)	800–900	483–569 (519)
Esophagus and body length	0.11†	0.10–0.11†	0.07†	0.08–0.11 (0.10)	0.06†	0.07
Nerve ring‡	—	—	250	208–237 (221)	418	192–304 (239)
Cervical papillae‡	—	—	460	278–341 (306)	—	265–387 (339)
Excretory pore‡	300	300	440	278–325 (298)	633	265–369 (333)
Tooth	Absent	Absent	Absent	Poorly developed	Absent	Present
Spicule length	140–150	140–158	170	122–148 (134)	220–240	140–159 (147)
Branching of spicule % from anterior	0.66†	0.66†	0.58†	0.58–0.65 (0.63)	0.64†	0.64–0.70 (0.68)

* 1: Skrjabin et al. (1954) including parts of redescription by Theiler and Robertson (1915); 2: Theiler and Robertson (1915) from ostriches in South Africa; 3: Durette-Desset and Denke (1978) from an ostrich in Somalia; may be referable to *L. magnus*, see text; 4: Present study based on specimens from Texas, USNM 83439; n = 5; 5: Description by Gilbert (1937) reproduced by Skrjabin et al. (1954).
† Estimated from written description or published figure.
‡ Measured from anterior.

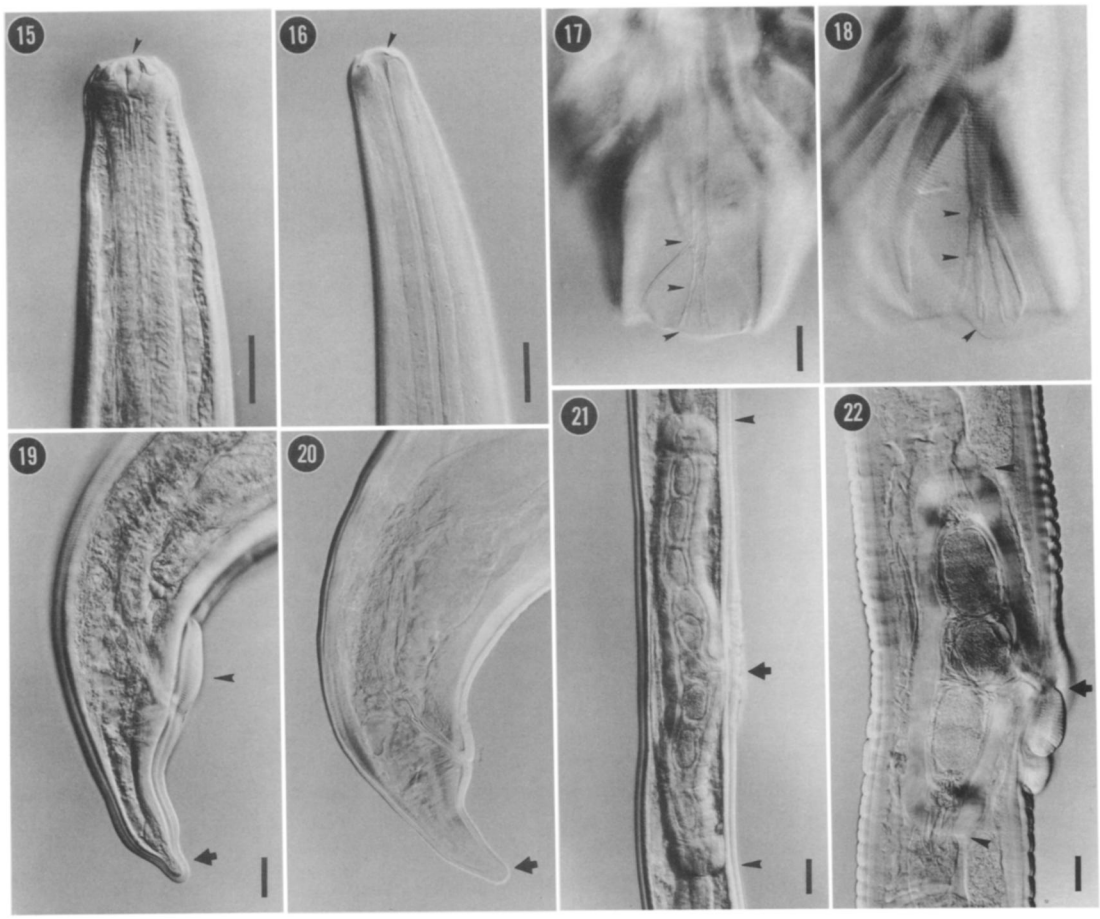
type and referring *L. hebrenicutus* and *P. nigeriae* (Baylis, 1928) to the new genus. *Libyostrongylus* was distinguished by a dorsal ray that split anterior to the origins of rays 9 and the terminal bifurcations (rays 10 and 11), and in which the tips of the latero-ventral (rays 3) and the externolateral (rays 4) rays were in proximity and the tips of the mediolateral (rays 5) were closer to those of the posterolateral (rays 6) rays. In contrast, *Paralibyostrongylus* was characterized by a dorsal ray in which rays 9 branched anterior to the terminal bifurcations ending in rays 10 and 11 and in which the tips of rays 4 were in proximity to those of rays 5.

Skrjabin et al. (1954) used the structure of the dorsal ray as

TABLE III. Comparison of female Libyostrongylinae from ostriches, including *Libyostrongylus douglassii* (Cobbold, 1882) (1–4), *L. magnus* Gilbert, 1937 (5), and *L. dentatus* n. sp.; ranges with mean values in parentheses.*

Character	1	2	3	4	5	*Libyostrongylus dentatus* n. sp.
Total length	5,100–5,600	5,630	7,900	5,105–6,031 (5,435)	7,560–11,430	10,205–12,730 (11,488)
Esophagus length	480–500	480–500	550	447–471 (458)	684–756	447–610 (545)
Esophagus and body length	0.09†	0.09†	0.07†	0.08–0.09 (0.08)	0.07–0.09†	0.04–0.05 (0.05)
Nerve ring‡	—	—	230	166–226 (198)	418	200–285 (254)
Cervical papillae‡	—	—	410	208–322 (278)	—	230–387 (323)
Excretory pore‡	300	300	390	198–283 (265)	633	208–380 (326)
Tooth	Absent	Absent	Absent	Poorly developed	Absent	Present
Vulva position	Ventral	Ventral	Ventral	Ventral	Ventral	Sublateral
Vulva % body length‡	0.85†	0.86†	0.77†	0.86	0.69–0.77†	0.92–0.93 (0.93)
Ovejector length	800§	300	1,365	377–463 (427)	—	702–933 (772)
Tail length	80	80	75	52–91 (73)	84–90	80–105 (92)
Tail inflation	Absent	Absent	Absent	Absent	Absent	Present
Egg length	50–74‖	59–74 (66)	75	65–70 (68)	80–92	52–62 (57)
Egg width	—	36–44 (41)	50	34–39 (36)	40–44	31–39 (34)
Eggs, no. anterior	—	30	—	18–29 (21)	—	29–71 (55)
Eggs, no posterior	—	15	—	6–13 (9)	—	9–20 (14)

* 1: Skrjabin et al. (1954) including parts of redescription by Theiler and Robertson (1915); 2: Theiler and Robertson (1915) from ostriches in South Africa; 3: Durette-Desset and Denke (1978) from an ostrich in Somalia; may be referable to *L. magnus*, see text; 4: Present study based on specimens from Texas, USNM 83439; n = 5; n = 25 for eggs; 5: Description by Gilbert (1937) reproduced by Skrjabin et al. (1954).
† Estimated from written description or published figure.
§ The 800 μm length appears to represent a mistake in transcription of part of Theiler and Robertson (1915) by Skrjabin et al. (1954).
‖ An egg length of 50 μm in *L. douglassii* is unreliable and is considered to be a fixation artefact in the type material of Cobbold (1882) as suggested by Theiler and Robertson (1915).
‡ Measured from anterior.



FIGURES 15–22. Comparison of key morphological characters for the identification of *L. dentatus* n. sp. and *L. douglassii*; scale bars = 20 μm, unless indicated otherwise. **15.** Cephalic extremity of *L. dentatus* showing prominent esophageal tooth, lateral view (pointer). **16.** Cephalic extremity of *L. douglassii* showing minuscule esophageal tooth (pointer). **17.** Dorsal ray in *L. dentatus* showing characteristic pattern of bifurcations (pointers). **18.** Dorsal ray in *L. douglassii* (same scale as Fig. 17) showing typical pattern of bifurcations (pointers). **19.** Tail in female of *L. dentatus,* with prominent cuticular swelling at level of anus (pointer) and digitate tip (arrow), lateral view. **20.** Tail in female of *L. douglassii* (same scale as Fig. 19) lacking cuticular inflation, and with rounded tip (arrow). **21.** Relatively long ovejector of *L. dentatus* (scale bar = 40 μm) showing region of sphincters and vestibule (between pointers) and position of vulva (arrow); note irregular inflations at level of vulva and numerous eggs in vestibule. **22.** Short ovejector of *L. douglassii* showing region of sphincters and vestibule (between pointers) and position of vulva (arrow); note irregular inflations near vulva and few eggs in the vestibule.

the primary criterion to separate the genera. However, Chabaud (1959) and Le Van Hoa (1959) regarded the genera as synonyms. The later contention was supported by the recognition of several species which appeared intermediate to *Libyostrongylus* and *Paralibyostrongylus,* e.g., *L. alberti* and *L. bathyergi* (Ortlepp, 1939), which had a "*Libyostrongylus*-type" dorsal ray, but "*Paralibyostrongylus*-type" lateral rays (Table IV).

Puylaert (1967) disregarded the structure of the dorsal ray as a diagnostic or phylogenetic character due to its putative variability among strongylate nematodes. Instead, generic designation was based on the relationships and position of the rays 3, 4, and 5. Secondarily, it was noted that species of *Libyostrongylus* were parasites of ratites, whereas *Paralibyostrongylus* were parasites of archaic mammals, lagomorphs, and primates; however, host association is not a valid generic criterion. This system was adopted by Durette-Desset and Chabaud (1977) with the establishment of the subfamily Libyostrongylinae and in the keys developed by Durette-Desset (1983, 1985) for the Trichostrongylidae. Under this system, 3 species currently referred to *Paralibyostrongylus* have a "*Libyostrongylus*-type" dorsal ray (Table IV). Among these species, *P. kalinae* exhibits a lateral ray pattern in which rays 3, 4, and 5 are equidistant (Durette-Desset et al., 1992), and thus is not clearly definable as *Paralibyostrongylus.* The pattern of the lateral rays in species of *Libyostrongylus* is consistent with the original generic diagnosis (Ortlepp, 1939) and that of Puylaert (1967); however, in specimens of *L. dentatus* the dorsal ray is of the "*Paralibyostrongylus*-type" (Table IV).

In contrast to the system presented by Durette-Desset (1983), keys developed by Gibbons and Khalil (1982) relied solely on the pattern of bifurcations of the dorsal ray to separate *Libyostrongylus* and *Paralibyostrongylus.* Thus, based on this criterion, *P. kalinae, P. alberti,* and *P. bathyergi* would be placed in *Libyostrongylus,* and *L. dentatus* would be placed in *Paralibyostrongylus* (Table IV).

Resolution of this problem is beyond the scope of the present

TABLE IV. Comparison of some diagnostic characters among *Libyostrongylus* spp. and *Paralibyostrongylus* spp.*

	Dorsal ray†	Lateral rays‡	Tooth	Spicule§	Egg‖
Libyostrongylus					
L. douglassii (Cobbold, 1882)	L	L	Present	122–158	59–74
L. magnus Gilbert, 1937	L	L	Absent	220–240	80–92
L. dentatus n. sp.	P	L	Present	143–159	52–62
Paralibyostrongylus					
P. vondwei Ortlepp, 1939	P	P	Absent	246–252	60–65
P. alberti (Berghe, 1943)	L	P	Absent	176–184	68
P. bathyergi (Ortlepp, 1939)	L	P	Absent	156–162	60–63
P. cassonei (Durette-Desset and Denke, 1978)	P	P	Absent	250	50
P. hebrenicutus (Lane, 1923)	P	P	Absent	250	65
P. kalinae Durette-Desset et al., 1992	L	P/L#	Present	190	60
P. mordanti Le Van Hoa, 1959	P	P	Absent	250	70
P. nigeriae (Baylis, 1928)	P	P	Absent	200	–

* From original descriptions and/or detailed redescriptions: Cobbold (1882), Theiler and Robertson (1915), Lane (1923), Baylis (1928), Ortlepp (1939), Skrjabin et al. (1954), Le Van Hoa (1959), Durette-Desset and Denke (1978), Cassone et al. (1992), and Durette-Desset et al. (1992).
† L = "*Libyostrongylus* type" and P = "*Paralibyostrongylus* type" according to Ortlepp (1939) and Gibbons and Khalil (1982).
‡ L = "*Libyostrongylus* type" (ray 4 closer to ray 3) and P = "*Paralibyostrongylus* type" (ray 4 closer to ray 5) according to Puylaert (1967) and Durette-Desset (1983).
§ Length of spicules; not including measurement reported by Durette-Desset and Denke (1978) for *L. douglassii*.
‖ Length of egg; not including data from Cobbold (1882) for *L. douglassii*.
In *P. kalinae*, figures indicate that ray 4 is equidistant from rays 3 or 5, thus not typical of either *Libyostrongylus* or *Paralibyostrongylus* (see Durette-Desset et al., 1992).

work, and synonymy of these genera is not currently justified. *Libyostrongylus dentatus* is provisionally referred to this genus pending phylogenetic analysis of the Libyostrongylinae. Such analysis should reveal the relative importance of these discordant characters, among other morphological attributes, in defining monophyletic taxa. Either the dorsal ray will be found to be diagnostic (with variable position of the lateral rays) (Gibbons and Khalil, 1982), or the pattern of lateral rays will be useful in definition of these genera (with variation in bifurcations of the dorsal ray) (Durette-Desset, 1983). Analysis of the 11 species relegated to either *Libyostrongylus* or *Paralibyostrongylus* has direct implications for understanding the coevolution of these nematodes in ratites, archaic rodents, lagomorphs, and primates. Interpretation hinges on recognizing monophyly for these genera or the possibility that at least *Libyostrongylus* or *Paralibyostrongylus* could be paraphyletic.

The potential for widespread dissemination of *Libyostrongylus* spp. among ostriches is indicated by the history of the female (type host) from North Carolina. This 5.5-yr-old bird had been hatched and raised near Houston, Texas, where it was housed until 1990. In that year, it was transported to Oklahoma and in 1993 to North Carolina where both *L. douglassii* and *L. dentatus* now appear to be established. In this regard, 2 other birds are now known to be infected (based on fecal examination) on the farm near Raleigh, North Carolina. A more detailed history for these parasites in North Carolina is in preparation.

The presence of *L. dentatus* in flocks from Texas suggests that this may have been the area of origin for this nematode once it was established in North America. This is suggested because the parasite is present in both Texas and North Carolina, and the distribution would be compatible, based on the history of the type host, with transport from the former locality. Additionally, it is of interest that birds from some flocks in Texas had been imported directly from Tanzania in the late 1980s (T. Craig, pers. comm.). This latter region may represent the historical distribution of *L. dentatus* in sub-Saharan Africa and may correspond with the range of the subspecies *Struthio camelus massaicus* Neumann (see Freitag and Robinson, 1993). Additionally, *L. magnus* appears to have been found thus far only in the nominate subspecies, *S. camelus camelus* Linnaeus, in Ethiopia and possibly the Sudan. In contrast, *L. douglassii* was originally described from South Africa and may be endemic or more common in southern Africa in *S. camelus australis* Gurney (Cobbold, 1882; Thieler and Robertson, 1915). The possibility of a disjunct distribution for these species of *Libyostrongylus* coinciding with the contemporary subspecies of ostriches that radiated during the Pliocene and Pleistocene (see Freitag and Robinson, 1993) remains to be evaluated. However, extensive transport of ostriches in Africa over the past century could confound elucidation of the historical host and geographic distributions of this fauna.

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